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South African Journal of Botany 81 (2012) 81 – 94

SOUTH AFRICAN JOURNAL OF BOTANY

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Review

Invasion dynamics of *Lantana camara* L. (sensu lato) in South Africa

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Received 15 September 2011; received in revised form 25 April 2012; accepted 1 June 2012

Abstract

Lantana camara L. (sensu lato) has a wide range of impacts throughout its global invasive range. Here we review the mechanisms driving its invasion dynamics in South Africa at national (biome, habitat) and regional (within a protected area) scales. Although only three introduction events into South Africa have been recorded (the earliest in 1858), as of 1998 *L. camara* was found in over 2 million ha (total area), with a condensed area of about 70,000 ha. Moreover, *L. camara* is present in most of the country's major biomes and a diversity of habitats, confirming its broad ecological tolerance. Using correlative bioclimatic models, we show that under future climate conditions, *L. camara*'s range in South Africa could expand considerably over the coming decades. While human-mediated dispersal and climatic suitability have been crucial in shaping *L. camara*'s current broad-scale distribution in South Africa, dispersal by birds and along rivers are important drivers of invasion at landscape scales. For example, current evidence suggests that in the Kruger National Park, *L. camara* has spread primarily along rivers. We conclude with a discussion on the implications of the different invasion dynamics for biological control and management, and provide recommendations for future research.

Keywords: Biological invasions; Geographic distribution; Kruger National Park; Management

Contents

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doi:10.1016/j.sajb.2012.06.002

1. Introduction

Plant invasions are mediated by a combination of invasiveness (i.e. species traits), invasibility (i.e. characteristics of receiving habitats), and the history of introduction (e.g. propagule pressure and residence time) (Foxcroft et al., 2011; Lockwood et al., 2005; Richardson and Pyšek, 2006; Wilson et al., 2009). Certain intrinsic factors predispose particular plant species to becoming invasive (Sakai et al., 2001). For example, Baker (1965) suggested that weedy plant species tend to reproduce both sexually and asexually, have rapid growth from seedling to sexual maturity, and show high adaptability to environmental stress and heterogeneity, i.e. possess a broad ecological amplitude. Further examples of plant species characteristics that have been linked with invasive potential include plant height, life form (Goodwin et al., 1999), seed size (Rejmánek and Richardson, 1996), polyploidy (Pandit et al., 2011; te Beest et al., 2012) and the ease with which a species hybridizes (Ellstrand and Schierenbeck, 2000).

Similarly, habitats vary in the degree to which they can be invaded. In particular, at a local scale habitats that are frequently disturbed (such as riparian areas or those subject to human activities) are often inherently more prone to invasion than others (Fridley, 2011; Richardson et al., 2007). However, identifying and measuring variation in invasibility across landscapes can be difficult, particularly if key factors (e.g. disturbance rates and fluctuating resource levels) vary over short geographic distances (Fridley, 2011).

Additionally, the origin of introduced propagules and the number, timing, and geographic location of introduction events act to determine both the success of an introduction and the rate of spread of an invasion (Lockwood et al., 2005; Wilson et al., 2009).

It is therefore evident that no simple predictor of invasion success prevails. Nonetheless, attempting to unravel which factors play a role in the invasion success for a particular invader provides insights that are useful for management (Sakai et al., 2001).

Lantana camara L. (sensu lato), a notorious global invader, has spread rapidly in many of the 60 regions of the world to which it has been introduced by humans (Day et al., 2003) and is listed among the world's one hundred worst invasive species (Lowe et al., 2000). It is considered a Weed of National Significance (WONS) in Australia, meaning that it displays exceptional invasiveness, potential for spread, and potential negative economic and environmental impacts (Clark et al., 2004). In a recent global review of invasive trees and shrubs, *L. camara* was found to be one of the most widespread invasive alien woody shrub species globally, being recorded as invasive in 12 of the 15 regions assessed (Richardson and Rejmánek, 2011). *L. camara* is one of the most conspicuous invaders in savanna ecosystems worldwide (Foxcroft et al., 2010).

Given *L. camara*'s global status as a species of considerable concern, it is not surprising that it has been extensively studied. A search for "*Lantana camara*" in Thomson-Reuters ISI Web of Science for the period 2000–2010 returns 366 publications, of which 174 have "*Lantana camara*" in the title. Much of the available knowledge of the species has accumulated recently, and is predominantly associated with biological control efforts (for a recent South African review see Urban et al., 2011), management (Bhagwat et al., 2012), ethnopharmacology (Ali-Emmanuel et al., 2003; Sathish et al., 2011), and phytochemistry (Kumar et al., 2011; Misra and Laatsch, 2000; Zoubiri and Baaliouamer, in press). However, despite this wealth of literature and its relevance to the South African situation, there has been no recent assessment of the invasion dynamics of *L. camara* in the region.

This paper reviews *L. camara* invasions in South Africa, with particular reference to known drivers of invasive success. Specifically, we aim to explain the processes and factors that have contributed to the successful invasion of the species, using a framework developed for invasion ecology; and to model distribution patterns across biomes, ecoregions, and under current and changing climate scenarios. We draw on information on *L. camara* invasions from other parts of the world (Day et al., 2003; Sharma et al., 2005) to provide the context within which the South African invasion will be examined. At a more localized scale, we investigate the progression of spread and management of *L. camara* in South Africa's flagship protected area, the Kruger National Park (KNP), a site where the invasion dynamics of *L. camara* have been studied in more detail than elsewhere in the country.

2. *L. camara* L. (sensu lato)

2.1. Origin

L. camara L. (sensu lato) (Verbenaceae), referred to in this paper as *L. camara*, is a complex of many horticultural hybrids

and a few wild *Lantana* species (Sanders, 1987, 2006). As originally described by Linnaeus in 1753, the genus *Lantana* contained six species from South America and one from Ethiopia (Ghisalberti, 2000). However, between 40 and 150 species and sub-specific entities are currently recognized (Day et al., 2003; Stirton, 1977). The capacity of many taxa to hybridize with others in the genus means that the taxonomy of the weedy complex remains problematic (Sanders, 2006; Urban et al., 2011).

Dutch explorers first collected *Lantana* spp. in the 1640s from South America and introduced plants to European gardens (Stirton, 1977). As popular ornamentals, numerous hybrid forms were later distributed worldwide (Howard, 1970; Morton, 1994; Stirton, 1977). The dominant parents of the hybrid forms are considered to be *L. camara* L. subsp. *aculeata* from the West Indies and *L. nivea* Vent. subsp. *mutabilis* from southern Brazil (Sanders, 2006). This morphological classification is congruent with recent molecular genetic research (see review by Urban et al., 2011). In its native range *L. camara* grows in small clumps in moist habitats. Although populations are found scattered along roadsides and in open fields, it is not considered weedy (Day et al., 2003). The invasion history of *L. camara* is well documented in some countries (Table 1), but poorly in others. In many of these countries *L. camara* was introduced as an ornamental plant, a hedge plant, or for use in folk medicine or mulch (Ghisalberti, 2000).

2.2. Impacts

2.2.1. Global

L. camara has been documented to cause a wide range of negative impacts around the world (Day et al., 2003; Sharma et al., 2005) (Table 1). It is a common weed of pastures, for example occupying 13.2 million ha of pastureland in India (Singh, 1996) where it reduces the grazing value of the land. Livestock death as a consequence of digesting fruit has also been reported (Wilson, 1995). It is also common in plantations in Fiji, Indonesia, Nicaragua, Sri Lanka, and Turkey, affecting a variety of crops (Table 1). Due to its fast growth, unpalatable nature, and allelopathy, *L. camara* is able to outcompete native species. It thus has conservation impacts, for example, in Australia, where *L. camara* adversely affects ca. 1300 native species (Anthony, 2008; Gentle and Duggin, 1997).

It is known that widespread and dominant invasive species not only have the potential to replace native flora, but also have direct impacts at other trophic levels by changing the habitat of animals (te Beest et al., 2009). *L. camara* has invaded large expanses of land in Kenya where it threatens the habitat of the sable antelope (Nanjappa et al., 2005) and affects bird habitats by altering community composition in India (Aravind et al., 2010). In tropical regions *L. camara* harbors pests that affect human health by providing shelter during the day for tsetse flies (*Glossina* sp.), which are vectors for African sleeping sickness (Mack and Smith, 2011; Table 1).

2.2.2. In South Africa

In 1962, a survey showed that *L. camara* had invaded between 25,000 and 30,000 ha of land in South Africa (Stirton, 1977; Wells and Stirton, 1988). By 2000, Le Maitre et al. (2000) reported that the species had invaded a total area of 2 million ha in the country, with a combined condensed area of almost 70,000 ha. This suggests a sixty-fold increase over five decades, although the two surveys used different methods. The latest national-level assessment, again using different methods, estimates the invaded area as about 560,000 ha (Kotze et al., 2010; Urban et al., 2011).

Expanding thickets obstruct access to water sources (Urban, 2010) and lowers water quality e.g., in the Hartenbos and Klein Brak River catchments in the Western Cape Province (River Health Programme, 2003). Although there is little empirical evidence of direct impacts on biodiversity, *L. camara* invasions in South Africa have been linked to decreased invertebrate diversity (Samways et al., 1996), and reduced grazing potential of up to 80% where stands are very dense (Van Wilgen et al., 2008). *L. camara* contains icterogenic triterpines which causes jaundice and photosensitization (Vahrmeijer, 1981), and has been documented to cause human and livestock mortality following fruit consumption (Wells and Stirton, 1988).

3. Mechanisms driving the invasion of *L. camara* in South Africa

Many conceptual frameworks have been developed to describe the processes and characteristics mediating the invasive potential and spread of a given species at particular spatial scales (Drake et al., 1989; Lodge, 1993; Richardson et al., 2000). Foxcroft et al.'s (2011) unified framework recognizes species traits that may enhance or decrease invasive potential (e.g. reproductive ability) as well as the susceptibility of recipient environments (e.g. the absence or presence of natural enemies in the receiving area). The framework includes spatial and temporal factors (defined as "system context") which link the species to the receiving habitat. We apply this framework to describe the progression of invasion of *L. camara* in South Africa (Fig. 1).

3.1. Species traits

Due to extensive breeding and intra and inter-specific hybridization, *L. camara* displays high morphological variation (Binggeli, 2003; Spies, 1984) and consequently over 50 varieties are recognized in South Africa alone (Spies and Stirton, 1982a,b). Morphological and ecological characteristics that have contributed to its successful spread in South Africa (as in other areas) are described in Fig. 1. These include prolific flowering and production of fleshy fruit throughout the year (Euston-Brown et al., 2007; Gujral and Vasudevan, 1983), features that are particularly important as frugivorous birds are important dispersal vectors. Endozoochory (i.e. the dispersal of seeds after passage through the vertebrate gut) has been shown to increase seed germination rates and vigor (Jordaan et al., 2011).

Table 1
Known distribution, introduction dates, and associated impacts of *Lantana camara* in different regions of the world. * Estimates of invaded areas are listed where available.

Region	Initial/early introduction records	Associated impacts and extent of invasion (*)
Australia	First reported by 1841 (Van Oosterhout et al., 2004)	Allelopathic suppression of indigenous plant species (Gentle and Duggin, 1997; Osunkoya and Perrett, 2011), poisonous in agricultural areas (Culvenor, 1985); consumption of fruit by humans have resulted in death (Morton, 1994) *4 million ha (Holm et al., 1991)
Bangladesh	Introduced early 19th century (Bansal, 1998)	Allelochemicals inhibit germination and initial growth of agricultural crops such as *Oryza sativa* and *Triticum aestivum* (Hossain and Alam, 2010)
Cook Island	First reported in 1969 (Fosberg, 1972)	Forms dense thickets on waste and fallow areas in the lowlands (McCormack, 2007)
Fiji	First reported around 1971 (Thaman, 1974)	A major weed of coconut plantations and pastures, reduced grazing land by 50% (Mune and Parham, 1967), livestock poisoning have been reported (Wilson, 1995)
Hawaii	Recorded as early as 1898 (Thaman, 1974)	Loss of large expanses of native vegetation (Diaz, 2010) *160,000 ha (Holm et al., 1991)
India	Introduced early 19th century (Thakur et al., 1992)	Harbors malarial mosquitoes (Day et al., 2003); affects bird community structure by decreasing bird diversity (Aravind et al., 2010), problematic in tea plantations (Holm et al., 1991) *13.2 million ha of pasturelands (Singh, 1996)
Indonesia		Problematic in tea plantations and a serious weed in coffee plantations and rice fields (Nanjappa et al., 2005)
Island of Rodrigues	Introduced in 1930 (Kueffer and Mauremootoo, 2004)	Invades rangelands (Kueffer and Mauremootoo, 2004)
Israel	Introduced as an ornamental, exact date unknown (Danin, 2000)	A threat to local flora in En Gedi and common in date plantations in Jordan-Dead Sea–Arava Rift Valley (Danin, 2000)
Kenya		Replacement of native pastures; threatening the habitat of sable antelope (Walton, 2006)
Madagascar	First reported in 1898	*100,000 ha (Binggeli, 2003)
Mauritius	Early records suggest 1837 (Kueffer and Mauremootoo, 2004)	
New Zealand	Introduced as a garden plant in 1890 (Peng et al., 1999)	Weed in agricultural ecosystems
Nicaragua		A weed in cotton fields (Holm et al., 1991)
Pitcairn Island	First reported in 1928 (Thaman, 1974)	
Philippines		Problematic in coconut (Cock and Godfray, 1985) and pineapple (Holm et al., 1991) plantations
Rwanda		Harbors tsetse flies (Day et al., 2003)
Samoa	Recorded as early as 1898 (Thaman, 1974)	Allelopathic effects on milkweed vine (*Morrenia odorata*), a weed in banana plantations (Holm et al., 1991)
South Africa	First recorded in 1858 in the old Cape Town Gardens (McGibbon, 1858)	Death of livestock and humans reported (Wells and Stirton, 1988), decreased invertebrate diversity (Samways et al., 1996), regeneration via allelopathy (Van Wilgen et al., 2001) *70,000 ha condensed area (Le Maitre et al., 2000)
Sri Lanka		A weed of coconut plantations (Sahid and Sugau, 1993)
Tanzania		Thickets provide breeding ground for tsetse flies, vectors of trypanosomiasis (Leak, 1999; Day et al., 2003).
Trinidad		A weed of coconut plantations (Holm et al., 1991)
Turkey		A weed of cotton plantations (Holm et al., 1991)
Uganda		Thickets provide breeding ground for tsetse flies, vectors of trypanosomiasis (Leak, 1999; Day et al., 2003).

L. camara also reproduces vegetatively and possibly also via self fertilization. Vegetative reproduction occurs by a process called layering, in which horizontal stems and cuttings take root when in contact with moist soil or leaf litter (Walton, 2006). Conflicting reports of self-compatibility in *L. camara* exist. Mohan Ram and Mathur (1984) and Neal (1999) considered the species to be self-compatible, albeit dependent on insect pollination. However, some varieties are unable to self-pollinate under laboratory conditions (Barrows, 1976). Due to extensive horticultural selection it is likely that self-compatibility may also be affected by polyploidization.

Polyploidization, whereby chromosome doubling occurs, is a major evolutionary process in plants. Moreover, unequal chromosome numbers (such as in triploids) may lead to complications of bivalent pairing during meiosis and therefore the formation of unviable gametes for sexual reproduction (Parisod et al., 2010). Polyploidy also has important consequences for invasiveness in plants (te Beest et al., 2012). A recent global

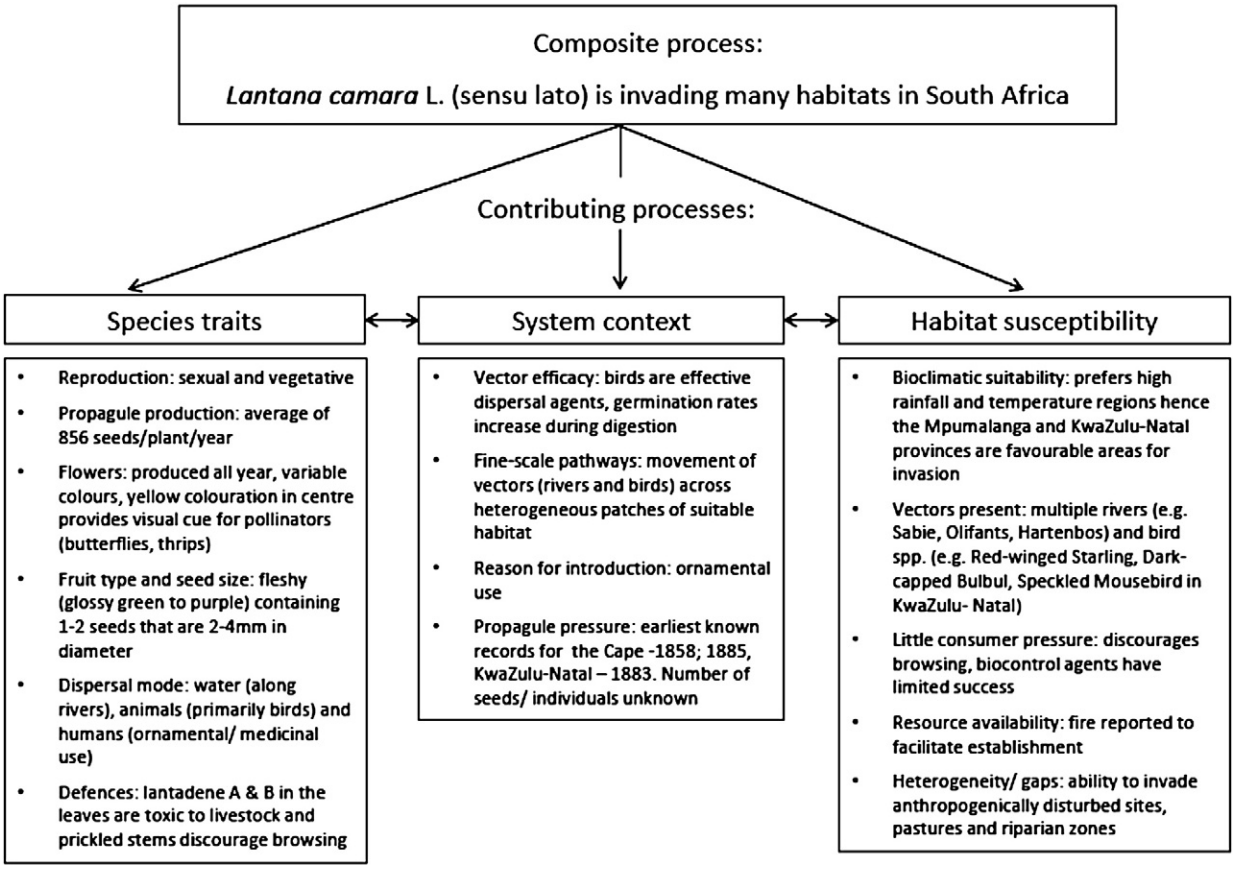

Fig. 1. A framework for the progression of invasion of *Lantana camara* in South Africa, showing the processes that contribute to its successful invasion. References are given in the text where each point is discussed. The framework structure follows Foxcroft et al. (2011).

review of ploidy levels among invasive and rare, localized, plants showed a positive correlation between polyploidy and invasiveness (Pandit et al., 2011). Polyploids have the potential to exhibit higher phenotypic plasticity, higher genetic diversity, and a greater tolerance to stress and changing environmental conditions, contributing to their potential for invasion (te Beest et al., 2012).

High variation in ploidy levels exists in *L. camara* (Brandao et al., 2007; Sanders, 1987), with polyploid individuals in the Carribean shown to be weedier, more widely distributed, and occupying a wider range of habitats than their diploid counterparts (Sanders, 1987). A cyto-taxonomic study of *L. camara* populations in South Africa revealed extreme ploidal diversity with chromosome numbers ($2n=22$) ranging from diploid to triploid, tetraploid, pentaploid, and hexaploid derivatives (Spies, 1984). Interestingly, frequent hybridization between different ploidy levels does occur, indicating that reproductive isolation between different ploidy levels is not complete (Spies, 1984).

3.2. Initial introductions and spread

The first record of *L. camara* in South Africa is from 1858 when four *Lantana* species of unknown origin were reported growing in the Cape Town Botanical Gardens (McGibbon, 1858). The second known introduction event was to KwaZulu-Natal from Mauritius in approximately 1883, as an ornamental plant (Morton, 1994). Just 2 years after the introduction to KwaZulu-Natal, an additional introduction to the Cape occurred, this time from Europe (Stirton, 1977). We could find no other records of introduction of *L. camara* to South Africa. However, the diversity of cultivars currently found in South Africa suggests that either additional unrecorded introductions were made from other parts of the world (Howard, 1970; Cilliers and Neser, 1991), or that the initial introductions contained considerable genetic diversity.

Following its introduction, plants were widely distributed around the country as ornamentals and, given suitable conditions, seeds were spread by frugivorous birds from wherever *L. camara* was planted. By 1946, *L. camara* was declared a dangerous weed and pest in agricultural ecosystems in KwaZulu-Natal, requiring control (Morton, 1994).

3.3. Current distribution

L. camara is naturalized in all but the driest and most heavily frosted parts of South Africa. Widespread, high-density populations are largely restricted to the eastern parts of the country (Fig. 2a), where it invades warm, moist subtropical and temperate areas in Mpumalanga, KwaZulu-Natal, and the Eastern Cape provinces. The distribution pattern in South Africa is similar to that of several other important invasive plant

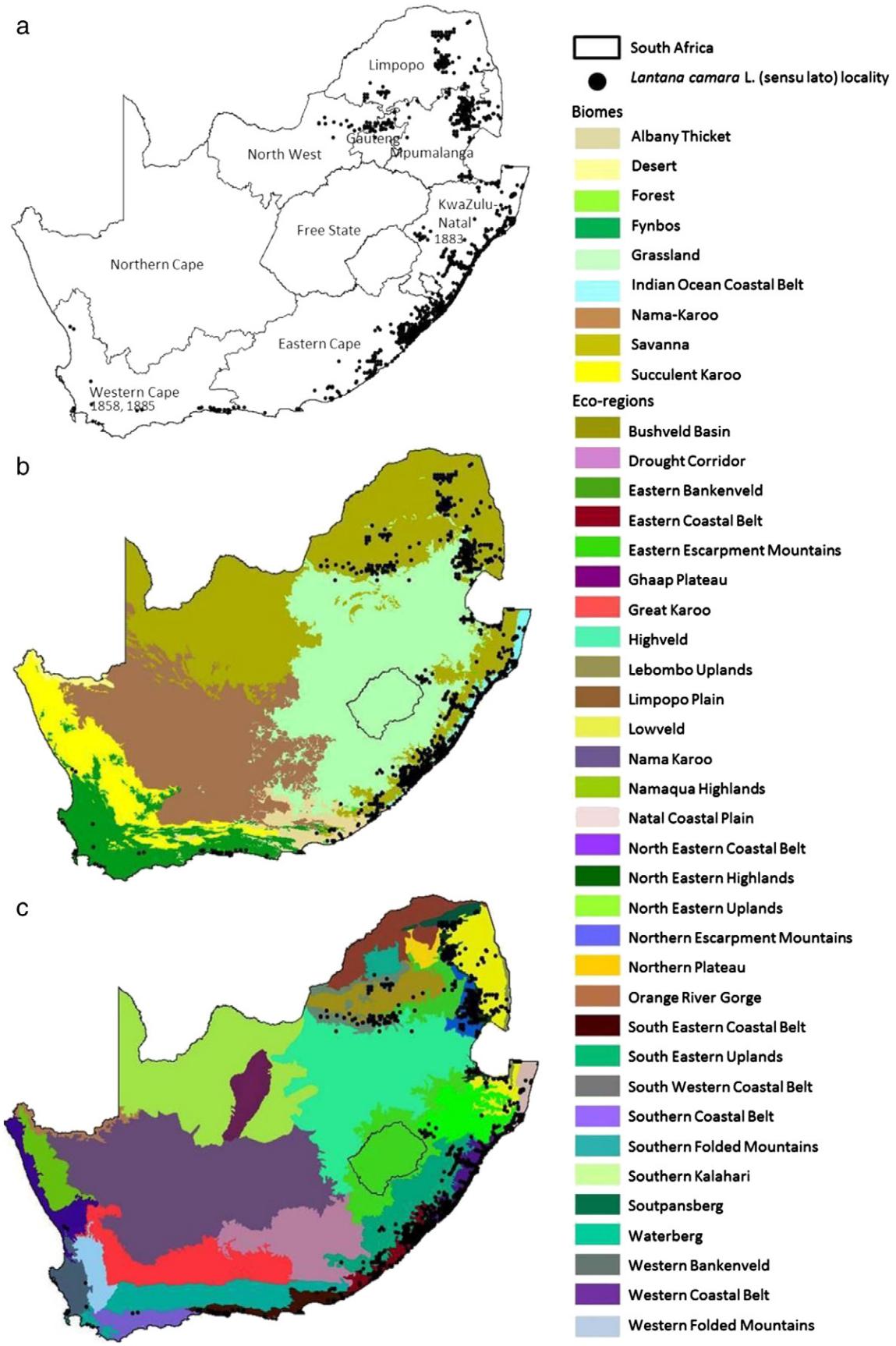

Fig. 2. Distribution of *Lantana camara* across (a) provinces, (b) biomes, and (c) ecoregions of South Africa (distribution data obtained from SAPIA, biome and ecoregion layers obtained from Mucina and Rutherford (2006)).

species, including *Acacia mearnsii* De Wild., *A. melanoxylon* R. Br., *Ricinus communis* L. and *Solanum mauritianum* Scop.; these species form one of nine "species clusters" defined on the basis of the environmental correlates of current distribution patterns (Richardson et al., 2004). In the drier parts of South Africa, *L. camara* generally only survives in gardens where they are maintained in microhabitats as ornamentals (Cilliers and Neser, 1991) or along rivers. Consequently, although the species is present in the Northern Cape and Free State provinces, no naturalization has been recorded in these regions (Henderson, 2001, 2007). In the Western Cape, naturalized *L. camara* is largely restricted to riparian zones (Meek et al., 2010) and areas adjoining suburban gardens (Alston and Richardson, 2006), and these populations are not as abundant or dense as in warm and wet provinces (Mpumalanga and KwaZulu-Natal).

Of concern however, is the large number of different landscape or vegetation types across which *L. camara* occurs. *L. camara* is present in 7 out of 9 terrestrial biomes in South Africa (Fig. 2b), and its distribution does not follow biome boundaries, typical of invasive species that invade riparian zones and a range of disturbed habitats (Richardson et al., 2004, 2007). However, the species is particularly prominent in the Savanna and Indian Ocean Coastal Belt biomes (Fig. 2b). At a finer scale, it is also found in two-thirds of all the ecoregions in South Africa (Fig. 2c). The diversity of biomes and ecoregions invaded by *L. camara* in South Africa shows that it can survive across a range of ecological gradients and communities. Moreover, at the local scale, multiple habitats are invaded (see Figs. 1 and 3), providing further evidence of its wide ecological tolerance. *L. camara* prefers anthropogenically disturbed areas (Richardson et al., 2004) such as roadsides and degraded land (Baars and Neser, 1999), pastures, bushveld (Van Wyk and Van Wyk, 1997), and riparian areas (Meek et al., 2010).

3.4. Bioclimatic suitability

Using the "most limiting factor" analysis implemented in DIVA-GIS 7.5 (Hijmans and Graham, 2006), we determined that of the 19 available BioClim variables, two rainfall (precipitation of warmest quarter and precipitation of coldest quarter) and three temperature (seasonality, mean temperature of warmest quarter, mean temperature of coldest quarter) variables are the most correlated to the distribution of *L. camara* in South Africa. We used maximum entropy (MAXENT) species distribution models to determine: 1) whether the current distribution of the species in South Africa represents all suitable climatic ranges or whether unoccupied but suitable, bioclimatic regions still exist; and 2) whether the suitable bioclimatic range of the species will expand, or retract, under a future climate change scenario. Naturalized occurrence records from the Southern African Plant Invaders Atlas (SAPIA; Henderson, 2007), gridded climate variables, and Köppen–Geiger vegetation classes were used to model the current and projected future bioclimatic range of *L. camara* in South Africa (see Supplementary data in Appendix A).

Bioclimatic modeling using current climate conditions shows that the coastal areas in the Eastern Cape and KwaZulu-Natal

Fig. 3. Representative habitats invaded by *Lantana camara* in South Africa. (a) invasion along a river in the Kruger National Park, (b) dense populations along a gravel road, Da Gama Dam, Mpumalanga, (c) along the Eerste River, Stellenbosch, Western Cape, where it is widespread but not abundant, (d) in a disturbed area between a fence line and railway, Kloof, KwaZulu-Natal, (e) along a highway, near Grahamstown, Eastern Cape, (f) at the edge of the Knysna forest, Western Cape. Photographs: a, b) Waafeka Vardien, c) Clifton Meek, d) David Richardson, e) John Wilson, and f) Haylee Kaplan.

provinces, and large parts of Mpumalanga and Limpopo are highly suitable for *L. camara*, in line with the known naturalized occurrences of the species in South Africa (Fig. 4a). This suggests large areas suitable for expansion in the KZN midlands. When a future (year 2050) climate scenario is considered, an increase in suitability is predicted in areas where the species is already present or invasive. This indicates that the suitable geographic range of the *L. camara* is likely to increase, although not to many new and geographically distinct regions (Fig. 4b). The species is already present in many areas with currently sub-optimal climatic conditions, usually in refuges such as riparian zones or human-modified habitats that are less affected by macro-climatic parameters than are more natural habitats. As such, there is the potential for even further rapid expansion as climatic conditions change.

4. Management efforts

4.1. Management of L. camara globally

Despite *L. camara*'s major ecological and economic impacts in many parts of the world, no standard methods have emerged for effective management of the species. This may be because the species occurs across such a wide range of vegetation types and land-uses, where perceptions of the species as a weed, management goals and available resources differ considerably (Day et al., 2003). Suites of methods are often used, the particulars of which are dependent on the land use, extent and density of the invasive populations, accessibility to invaded areas, economic value of land, and the associated costs (Day et al., 2003). Because biological control is not influenced solely by these constraints, it is considered the most desirable control option. This is especially true in countries with widespread invasions which sometimes occur in inaccessible sites, and poor financial resources for on-going mechanical, chemical or other control measures.

However, classical biological control has been confounded by the diverse hybrid composition of the *Lantana* complex. Biological control of *L. camara* started in 1902, when 23 insect agents were imported from Mexico to Hawaii (Day et al., 2003); eight of these established successfully in the field. To date, more than 40 insect agents have been released globally (Day et al., 2003), with variable success. Hawaii, Australia and South Africa have each released more than 20 insect agents. Interestingly, control on islands has been more effective than in continental regions (Julien and Griffiths, 1998), presumably because there are fewer indigenous natural enemies of the biocontrol agents. The most effective insect agents so far are defoliating herbivores, e.g. *Teleonemia scrupulosa* Stål and *Uroplata girardi* Pic. *T. scrupulosa* has successfully established in 29 of the 31 countries where it has been introduced and *U. girardi* in 24 of 26 countries (Day et al., 2003). Although research on the biological control of *L. camara* is continuing, this form of control is currently not contributing substantially to overall management efforts (Hoffmann, 1995), though the average degree of control achieved by *L. camara* biocontrol agents in inland areas is estimated to be about 26% globally (Zalucki et al., 2007). Host specificity and varietal preference of released agents, climatic suitability of the region for released agents, the number of agents introduced, and the extent of the invaded area appear to limit the success of biological control (Zalucki et al., 2007).

Mechanical control is only effective for small stands and is contingent on continuous and meticulous follow-up. Methods for removal of *L. camara* include the use of bulldozers and tractors to remove plants (Day et al., 2003). This method minimizes disturbance to nearby vegetation and is effective in killing the plants, but is only feasible where the plants are small, and where they occur in small, isolated clumps. These methods are impractical where large areas are invaded, for example in Australia. This is not the case in very dry areas,

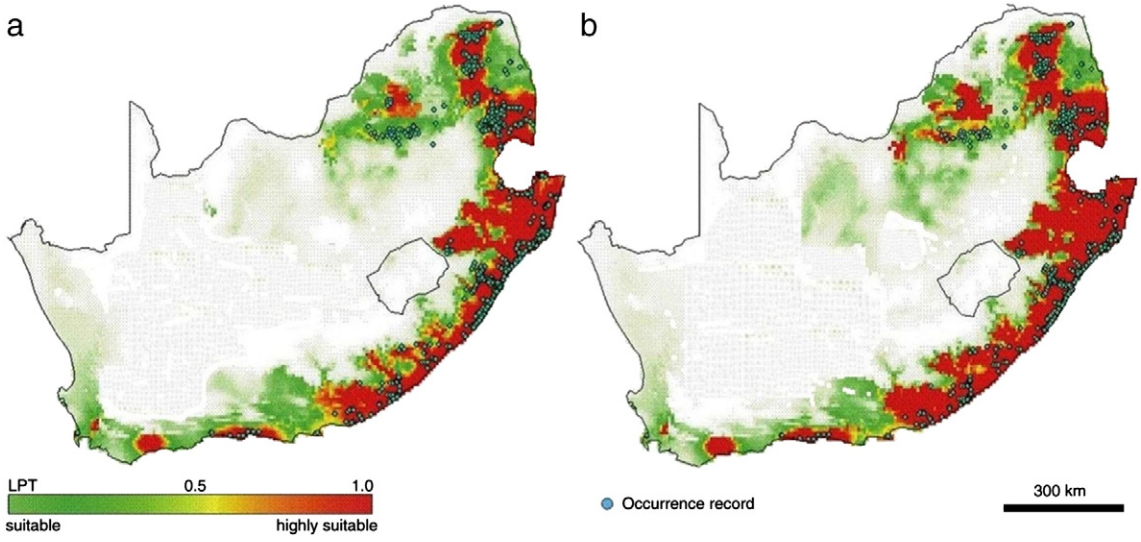

Fig. 4. Envelopes of (a) current and (b) future (2050) bioclimatic suitability for *Lantana camara* L. (sensu lato) in South Africa based on 10 replicate, MaxEnt models. Models were developed using South African records of naturalized populations, 5 Bioclim variables (Bio 4, 10, 11, 18, 19) and Köppen–Geiger vegetation classes to select pseudo-absence data. See text (Section 3.4) and Appendix A for further details.

where it is possible to first bulldoze and immediately plant pasture grass, and spray herbicide on any re-growth (Morton, 1994). In India, grubbing, the slashing of branches, and extensive digging of the root system, are used to control the weed in forest ecosystems (Love et al., 2009). However, this is disadvantageous as the soil is disturbed and *L. camara* seeds are exposed to light, leading to stimulation of germination and establishment of seedlings, as well as coppicing from slashed branches (Love et al., 2009).

Chemicals are an effective but expensive method for *L. camara* control and effectiveness depends on plant size, time of application, mode of application, and the use of surfactant. Various herbicide treatments are used and are said to be most effective when applied as a foliar spray or to the base of the stems and cut stumps (Graaff, 1987). Some herbicides (belonging to the phenoxy acid, benzoic acid, and pyridine groups; Day et al., 2003) appear to be more effective on particular forms of lantana (Swarbrick et al., 1995).

4.2. Management of *L. camara* in South Africa

4.2.1. Biological control

Biological control of *L. camara* in South Africa started in 1961 (Baars et al., 2003). During the period between 1961 and 1995, 19 insect species were released (Julien and Griffiths, 1998). Since then a further five agents have been released, and of the total number of agents released, 13 have established (Klein, 2011). Generally, the agents released have had limited success, although five species have been shown to suppress *L. camara* growth and reproduction in certain areas: *Octotoma scabripennis* Guérin-Méneville, *U. girardi* and *T. scrupulosa* (Cilliers, 1987; Day and Neser, 2000) as well as *Ophiomyia camarae* Spencer and *Aceria lantanae* Cook (Urban et al., 2011). These agents are estimated to be collectively reducing the rate of growth and reproduction of *L. camara* by approximately 40%, which greatly reduces the frequency and cost of mechanical and chemical control actions (Urban et al., 2011). The inability of biological control agents to stop *L. camara* from increasing its range and density is attributed to the variability of the weed, high incidence of parasitism of control agents, and the wide range of climatic conditions over the plant's range in South Africa (Cilliers and Neser, 1991; Day and Neser, 2000), as well as induced resistance, allelochemicals and alloploidy (Urban et al., 2011). Cost–benefit analysis indicated that the return on investment for lantana biocontrol research in SA was eight to 34 fold (Van Wilgen et al., 2004). The value of the reduction in the rate of loss of pasturage and ecosystem services, achieved by the lantana biocontrol agents in SA, was conservatively estimated to be at least 7 million ZAR/annum (Urban et al., 2011).

Over the last two decades, the potential of fungal pathogens as control agents has also been explored, and in 2001 permission was granted to release the leaf-spot fungus *Passalora lantanae* Chupp (formerly in *Mycovellosiella*), collected from Florida, USA (Den Breeÿen and Morris, 2003). It was released in the Eastern Cape, KwaZulu-Natal and Mpumalanga (Euston-Brown et al., 2007), but failed to establish (Retief, 2010). Other pathogens currently under investigation include *Septoria* sp. and *Puccinia lantanae* Farlow (Klein, 2011).

4.2.2. Integrated control

The largest initiative in South Africa, using mechanical/physical and chemical control of *L. camara* falls under the government's Working for Water Programme (WfW). An estimated 180.6 million ZAR has been spent on *L. camara* clearing in South Africa by WfW between 1995 and 2008, with some indications that the total invaded area has declined as a result (Van Wilgen et al., 2012). Mechanical control methods used in WfW projects involve slashing and sometimes scraping by bulldozing. In areas with limited invasions, hand pulling of seedlings is employed (Euston-Brown et al., 2007).

At least 11 herbicides are registered for use on *L. camara* in South Africa (see Euston-Brown et al., 2007). The most widely used, and probably most successful approach is a combination of mechanical and chemical controls (Urban, 2010). This is done by cutting plants and immediately painting the stumps with an appropriate herbicide. Marais et al. (2004), reported that during 2002/03 the WfW cleared 5407 ha of *L. camara* at a cost of 572 ZAR/ha (totaling just over 3 million ZAR). The estimated follow-up cost for the same area was 7 million ZAR (approximately US$1 million), emphasizing the expensive nature of chemical (combined with manual) treatment for *L. camara* control.

5. Progression of *L. camara* invasions at a localized scale: the Kruger National Park (KNP) situation

Kruger National Park (KNP) is South Africa's flagship protected area for biodiversity conservation. In 1937 concern was expressed regarding the invasion of alien plant species in the park, but it was not until about 1958 that serious concerns arose, prompting a report to be submitted to the National Parks Board. The report stated that the invasion of plant species in general had to be curbed and that management would only be effective if species were targeted both in the park and at source populations beyond the park's boundaries (Joubert, 1986). The KNP Board then passed a resolution (No. 90 of 9th December 1958) whereby listed alien plants were declared undesirable. *L. camara* was included on this list and has remained on such lists since then (Joubert, 1986).

L. camara was first recorded in KNP in 1940 and was even planted extensively as an ornamental in tourist camps throughout the 1950s. More recently, *L. camara* has been recorded from nine tourist camps from which invasions are likely the result of the original ornamental plantings (Foxcroft et al., 2008a). It was subsequently also observed invading into the park along rivers (Martin and Foxcroft, 2002) from upper catchment areas that are highly invaded. It is considered a "transformer species" in the park (Foxcroft and Richardson, 2003), i.e. it alters the form, character and nature of the ecosystems over a substantial area comparative to the extent of that ecosystem (Richardson et al., 2000), with dense stands covering large areas in the park. While *L. camara* is present in most rivers and tributaries throughout the park, it is more

abundant in the southern region, especially along the Sabie and Crocodile Rivers (Fig. 5). A large flood event (1 in 75–100 years) in the Sabie River in 2000 (Foxcroft et al., 2008b) appears to have triggered large-scale invasive plant recruitment. The density of *L. camara* has, however, not increased substantially as a result of the flood event, largely due to the rapid and continued management efforts (personal observation, Llewellyn Foxcroft, note the spread seen in Fig. 5 was over a much longer time period and was influenced by an increase in survey effort).

Management of *L. camara* in the KNP has focused mainly on mechanical and chemical controls (Foxcroft et al., 2009). Efforts to determine the method with the least non-target effects in the park indicated that chemical control combined with manual control is the most cost effective and caused the least disturbance, and the smallest impact on biodiversity (Erasmus et al., 1993). Chemical control consisted of an application of imazapyr on freshly cut stumps and a follow-up operation by spot-spray application of glyphosate. The initial control required 25 person-days/ha with the follow-up control requiring 6.8 person-days/ha (Erasmus et al., 1993).

As with any localized invasion, the control of *L. camara* in KNP may potentially be improved through enhanced knowledge of dispersal patterns and spread dynamics, specifically through identifying sources in catchment areas of all the main river systems to aid in more effective management. Management efforts can then be directed to areas that will minimize spread and post-control re-invasion. While large stands in upper catchments appear to act as important sources for the continuing spread of *L. camara* along rivers in KNP, numerous scattered populations also exist, away from rivers and water courses (Fig. 5). These outlying foci are important for management in the whole-KNP context, as the eradication of small pioneering populations can be the most effective means of slowing and even preventing further spread (Moody and Mack, 1988).

6. Conclusions

Several plant traits, anthropogenic processes, and biogeographic characteristics have interacted to shape the successful invasion of *L. camara* in South Africa. The flowering phenology, amount of fruit produced, and the many seed dispersal agents are the dominant drivers of *L. camara* invasion in South Africa. This is because climatic conditions over a large portion of South Africa meet *L. camara*'s requirements year-round for flower and fruit production and seed germination. Thus, using spatially-explicit data to simulate invasion scenarios and to determine the geographical limits of *L. camara*, and show how population dynamics may be affected by

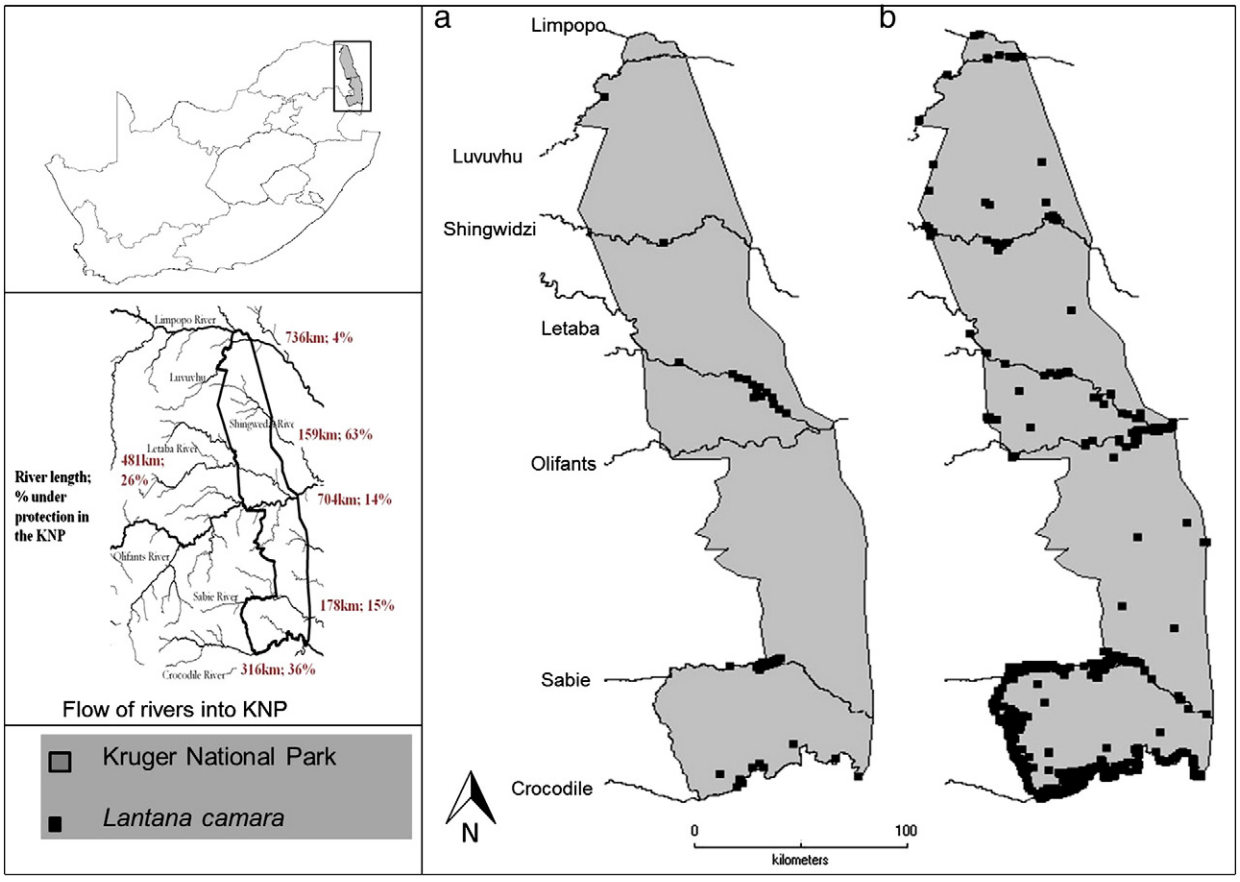

Fig. 5. The distribution of *Lantana camara* L. (sensu lato) in the Kruger National Park (KNP) based on (a) records from the KNP Invasive Alien Biota Section before 2000, and (b) Cybertracker data from 2000 to 2010 (see Foxcroft et al., 2009 for details). The top left insert on the figure shows the location of KNP within South Africa and the bottom left insert the configuration of major rivers within KNP.

changing climatic conditions, are important requirements for improving the management of the species. Management efforts would also benefit from applying mechanistic approaches, using data on traits, soil and biotic interactions to model potential distributions.

Birds disperse seeds across patches of heterogeneous habitats. The fact that *L. camara* discourages browsing because of its prickles and thorns, further enhances its ability to spread and persist in newly colonized areas. No studies in South Africa have measured the distances over which animals disperse *L. camara* seeds, but work in other regions have documented distances up to 1 km (Swarbrick et al., 1995). Rivers have also been shown to be important vectors of spread (Foxcroft and Richardson, 2003). However, these two dispersal vectors (animals and rivers) alone cannot explain the current distribution of *L. camara* invasions in South Africa. Human-aided dissemination has clearly shaped the current distribution. Deliberate dispersal by humans is likely to decrease in importance in the future as the horticultural industry has recognized and responded to the risks associated with trading and disseminating of potentially invasive lantana varieties. At a localized scale, however, it is clear that dispersal will continue through natural processes, and these need to be understood for future management. In particular, determining the configuration of suitable habitats within landscapes and patches where *L. camara* occurs may provide better insights for prioritizing regional control efforts. For example, in the Kruger National Park dispersal has occurred primarily along rivers rather than via long-distance dispersal by humans and other vertebrates. Given the known rates of natural dispersal via birds and rivers, large-scale movements by humans of once-important horticultural varieties, to regions of suitable climate must have primarily facilitated its rapid spread across South Africa.

The large number of genetically diverse entities within *L. camara* is an important obstacle for effective biological control, which can only be overcome by finding additional host-specific biocontrol agents. The suite of biocontrol agents already released in South Africa has been shown to have decreased the rates of growth and reproduction of lantana, and thus reduced the frequency and cost of mechanical plus chemical control. *Lantana* biocontrol research has been found to be highly cost-effective, and further work should be done on expanding the range of biocontrol agents.

Acknowledgments

We acknowledge financial support from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water (WfW) Programme through their collaborative project on “Research for Integrated Management of Invasive Alien Species”; Lesley Henderson (ARC-PPRI) for lantana distribution data from the SAPIA database; and Bruce Webber and Nobura Ota (CSIRO, Western Australia) for 5 min Köppen–Geiger vegetation layers. JLR acknowledges the Stellenbosch University’s Sub-committee B ‘Young Researchers Fund’ for funding and South Africa’s National Research Foundation’s (NRF) Thuthuka Programme (grant no. 76327). LCF and DMR acknowledge the NRF for incentive funding, and LCF received a grant from the UNESCO Man and Biosphere Young Scientists Initiative.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2012.06.002.

References

Ali-Emmanuel, N., Moudachirou, M., Akakpo, J.A., Quetin-Leclercq, J., 2003. Treatment of bovine dermatophilosis with *Senna alata*, *Lantana camara* and *Mitracarpus scaber* leaf extracts. Journal of Ethnopharmacology 86, 167–171.

Alston, K.P., Richardson, D.M., 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation 132, 183–198.

Anthony, D., 2008. Queensland leads national approach to lantana eradication. http://www.dpi.qld.gov.au/cps/rde/dpi/hs.xsl/30_10514_ENA_HTML.htm.

Aravind, N.A., Rao, D., Ganeshaiah, K.N., Shaanker, R.U., Poulsen, J.G., 2010. Impact of the invasive plant, *Lantana camara*, on bird assemblages at Male Mahadeshwara Reserve Forest, South India. Tropical Ecology 51, 325–338.

Baars, J.R., Neser, S., 1999. Past and present initiatives on the biological control of *Lantana camara* (Verbenaceae) in South Africa. African Entomology Memoir 1, 21–34.

Baars, J., Urban, A.J., Hill, M.P., 2003. Biology, host range, and risk assessment supporting release in Africa of *Falconia intermedia* (Heteroptera: Miridae), a new biocontrol agent for *Lantana camara*. Biological Control 28, 282–292.

Baker, H.G., 1965. Characteristics and modes of origin of weeds. In: Baker, H.G., Stebbins, G.L. (Eds.), The Genetics of Colonizing. Academic, New York, pp. 147–169.

Bansal, G.L., 1998. Allelopathic effects of *Lantana camara* on rice and associated weeds under the midhill conditions of Himachal Pradesh, India. In: Olofsdotter, M. (Ed.), Proceedings of the Workshop on Allelopathy in Rice. International Rice Research Institute, Manila, Philippines, pp. 133–138.

Barrows, E.M., 1976. Nectar robbing and pollination of *Lantana camara* (Verbenaceae). Biotropica 8, 132–135.

Bhagwat, S.A., Breman, E., Thekaekara, T., Thornton, T.F., Willis, K.J., 2012. A battle lost? Report on two centuries of invasion and management of *Lantana camara* L. in Australia, India and South Africa. PLoS One 7, e32407, http://dx.doi.org/10.1371/journal.pone.0032407.

Binggeli, P., 2003. Verbenaceae, *Lantana camara*, fankatavinakoho, fotatra, mandadrieko, rajejeka, radredreka, ramity. In: Goodman, S.M., Benstead, J.P. (Eds.), The Natural History of Madagascar. University of Chicago Press, Chicago, pp. 415–417.

Brandao, A.D., Viccini, L.F., Salimena, F.R.G., Vanzela, A.L.L., Recco-Pimentel, S.M., 2007. Cytogenetic characterization of *Lippia alba* and *Lantana camara* (Verbenaceae) from Brazil. Journal of Plant Research 120, 317–321.

Cilliers, C.J., 1987. The evaluation of three insect natural enemies for the biological control of the weed *Lantana camara* L. Journal of the Entomological Society of Southern Africa 50, 15–34.

Cilliers, C.J., Neser, S., 1991. Biological control of *Lantana camara* (Verbenaceae) in South Africa. Agriculture, Ecosystems and Environment 37, 57–75.

Clark, A., Van Oosterhout, E., Menzies, E., Haapakoski, H., Day, M., 2004. *Lantana*—at WoNS with the community? In: Sindel, B.M., Johnson, S.B. (Eds.), Proceedings of the 14th Australian Weeds Conference. Weed Society of New South Wales, Sydney, pp. 627–630.

Cock, M.J.W., Godfray, H.C.J., 1985. Biological control of *Lantana camara* in the Philippines. Journal of Plant Protection in the Tropics 2, 61–63.

Culvenor, C.C.J., 1985. Economic loss due to poisonous plants in Australia. In: Seawright, A.A., Hegarty, M.P., James, L.F., Keeler, R.F. (Eds.), Proceedings of the Australia–U.S.A. Poisonous Plants Symposium Brisbane, Australia, pp. 3–13.

Danin, A., 2000. The inclusion of adventive plants in the second edition of Flora Palaestina. Wildenowia 30, 305–314.

Day, M.D., Neser, S., 2000. Factors influencing the biological control of Lantana camara in Australia and South Africa. In: Spencer, N.R. (Ed.), Proceedings of the X International Symposium on the Biological Control of Weeds. Bozeman, Montana, USA, pp. 897–908.

Day, M.D., Wiley, C.J., Playford, J., Zalucki, M.P., 2003. *Lantana* current management status and future prospects. ACIAR, Canberra. Monograph 102.

Den Breeÿen, A., Morris, M.J., 2003. Pathogenicity and host specificity of *Mycovellosiella lantanae* var. *lantanae*, a potential biocontrol agent for *Lantana camara* in South Africa. Biocontrol Science and Technology 13, 313–322.

Diaz, S., 2010. Biodiversity and ecosystem services. In: Cleveland, C.J. (Ed.), Encyclopaedia of Earth. Environmental Information Coalition, National Council for Science and the Environment, Washington, D.C.. First published in the Encyclopaedia of Earth May 20, 2010; Last revised date November 6, 2010; Retrieved June 27, 2011.

Drake, J.A., Mooney, H.A., Di Castri, F., Groves, F., Kruger, F.J., Rejmánek, M., Williamson, M., 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, New York.

Ellstrand, N.C., Schierenbeck, K.A., 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences of the United States of America 97, 7043–7050.

Erasmus, D.J., Maggs, K.A.R., Biggs, H.C., Zeller, D.A., Bell, R.S., 1993. Control of *Lantana camara* in the Kruger National Park, South Africa, and subsequent vegetation dynamics. Brighton Crop Protection Conference: Weeds—1993, vols. 1–3, pp. 399–404.

Euston-Brown, D., Rathogwa, N., Richardson, D.M., 2007. Protocol based on Ecological criteria for Mesic Savannas and Sweet Grassveld for the Working for Water Programme. Report to the Working for Water Programme, Working for Water, Cape Town. .

Fosberg, F.R., 1972. List of vascular plants (reef islands of Rarotonga). Atoll Research Bulletin 160, 9–14.

Foxcroft, L., Richardson, D.M., 2003. Managing alien plant invasions in the Kruger National Park, South Africa. In: Child, L.E., Brock, J.H., Brundu, G., Prach, K., Pyšek, P., Wade, P.M., Williamson, M. (Eds.), Plant Invasions: Ecological Threats and Management Solutions. Backhuys Publishers, Leiden, The Netherlands, pp. 385–403.

Foxcroft, L.C., Parsons, M., McLoughlin, C.A., Richardson, D.M., 2008a. Patterns of alien plant distribution in a river landscape following an extreme flood. South African Journal of Botany 74, 463–475.

Foxcroft, L.C., Richardson, D.M., Wilson, J.R.U., 2008b. Ornamental plants as invasive aliens: problems and solutions in the Kruger National Park, South Africa. Environmental Management 41, 32–51.

Foxcroft, L.C., Richardson, D.M., Rouget, M., MacFadyen, S., 2009. Patterns of alien plant distribution at multiple spatial scales in a large national park: implications for ecology, management and monitoring. Diversity and Distributions 15, 367–378.

Foxcroft, L.C., Richardson, D.M., Rejmánek, M., Pyšek, P., 2010. Alien plant invasions in tropical and sub-tropical savannas: patterns, processes and prospects. Biological Invasions 12, 3913–3933.

Foxcroft, L.C., Pickett, S.T.A., Cadenasso, M.L., 2011. Expanding the conceptual framework of plant invasion ecology. Perspectives in Plant Ecology, Evolution and Systematics 13, 89–100.

Fridley, J.D., 2011. Invasibility of communities and ecosystems. In: Simberloff, D., Rejmánek, M. (Eds.), Encyclopedia of Biological Invasions. University of California Press, Berkley, pp. 356–360.

Gentle, C.B., Duggin, J.A., 1997. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. Plant Ecology 132, 85–95.

Ghisalberti, E.L., 2000. *Lantana camara* L. (Verbenaceae). Fitoterapia 71, 467–486.

Goodwin, B., McAllister, A., Fahrig, L., 1999. Predicting invasiveness of plant species based on biological information. Conservation Biology 13, 422–426.

Graaff, J.L., 1987. The seedfly *Ophiomyia lantanae* and other factors responsible for reducing germination in *Lantana camara* forms found in Natal. South African Journal of Botany 53, 104–107.

Gujral, G.S., Vasudevan, P., 1983. *Lantana camara* L., a problem weed. Journal of Scientific and Industrial Research 42, 281–286.

Henderson, L., 2001. Alien weeds and invasive plants. Plant Protection Research Institute Handbook, No. 12. Agricultural Research Council, Pretoria, p. 300.

Henderson, L., 2007. Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia 37, 215–248.

Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12, 1–10.

Hoffmann, J.H., 1995. Biological control of weeds: the way forward, a South African perspective. In: Stirton, C.H. (Ed.), British Crop Protection Council Symposium Proceedings No. 64: Weeds in a Changing World, pp. 77–89.

Holm, L.G., Plucknett, D.L., Pancho, J.V., Herberger, J.P., 1991. The World's Worst Weeds: Distribution and Biology. Krieger Publishing Company, Malabar, Florida.

Hossain, M.K., Alam, M.N., 2010. Allelopathic effects of *Lantana camara* leaf extract on germination and growth behaviour of some agricultural and forest crops in Bangladesh. Pakistan Journal of Weed Science Research 16, 217–226.

Howard, R.A., 1970. *Lantana camara*—a prize and a peril. American Horticultural Magazine 49, 31.

Jordaan, L.A., Johnson, S.D., Downs, C.T., 2011. The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants. Biological Invasions 13, 1917–1930.

Joubert, S.C.J., 1986. Master Plan for the Management of the Kruger National Park, vols. 1–6. National Parks Board, Skukuza, South Africa.

Julien, M.H., Griffiths, M.W., 1998. Biological control of weeds, A World Catalogue of Agents and Their Target Weeds Fourth edition. CABI Publishing, Wallingford, UK.

Klein, H., 2011. A catalogue of the insects, mites and pathogens that have been used or rejected, or are under consideration, for the biological control of invasive alien plants in South Africa. African Entomology 19, 515–549.

Kotze, I., Beukes, H., Van den Berg, E., Newby, T., 2010. National invasive alien plant survey. Report No. GW/A/2010/21 to the Department of Water and Environmental Affairs, Working for Water Programme. Agricultural Research Council—Institute for Soil, Climate and Water, Pretoria. Available from: http://sites.google.com/site/wfwplanning/assessment/Kotzeetal.%2C2010.pdf?attredirects=0.

Kueffer, C., Mauremootoo, J., 2004. Case studies on the status of invasive woody plant species in the Western Indian Ocean. 3 Mauritius (Islands of Mauritius and Rodrigues). Forest Health and Biosecurity Working Papers FBS/4-3E. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

Kumar, V., Naithani, S., Pandey, D., 2011. Optimization of reaction conditions for grafting of α-cellulose isolated from *Lantana camara* with acrylamide. Carbohydrate Polymers 86, 760–768.

Le Maitre, D.C., Versfeld, D.B., Chapman, R.A., 2000. The impact of invading alien plants on water resources in South Africa: a preliminary assessment. Water SA 26, 397–408.

Leak, S.G.A., 1999. Tsetse biology and ecology, their role in the epidemiology and control of trypanosomosis. CAB International, Wallington, U.K.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20, 223–228.

Lodge, D.M., 1993. Biological invasions: lessons for ecology. Trends in Ecology & Evolution 8, 133–137.

Love, A., Babu, S., Babu, C.R., 2009. Management of *Lantana*, an invasive alien weed, in forest ecosystems of India. Current Science 97, 1421–1429.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species - A selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group

(ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), p. 12.
Mack, R.N., Smith, M.C., 2011. Invasive plants as catalysts for the spread of human parasites. NeoBiota 9, 13–29.
Marais, C., Van Wilgen, B.W., Stevens, D., 2004. The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. South African Journal of Science 100, 97–103.
Martin, B.W., Foxcroft, L.C., 2002. First atlas of maps for invasive alien species within the Kruger National Park as in 2001. SANParks Report No. 01/02, Alien Biota Section, Scientific Services Section, Skukuza, Kruger National Park.
McCormack, G., 2007. Cook Islands Biodiversity Database, Version 2007.2. Cook Islands Natural Heritage Trust. Retrieved from http://cookislands.bishopmuseum.org.
McGibbon, J., 1858. Catalogue of plants in the botanic garden, Cape Town, Cape of Good Hope. Solomon, Cape Town.
Meek, C.S., Richardson, D.M., Mucina, L., 2010. A river runs through it: land-use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa. Biological Conservation 143, 156–164.
Misra, L., Laatsch, H., 2000. Triterpenoids, essential oil and photo-oxidative 28 13-lactonization of oleanolic acid from *Lantana camara*. Phytochemistry 54, 969–974.
Mohan Ram, H.Y., Mathur, G., 1984. Flower color changes in *Lantana camara*. Journal of Experimental Botany 35, 1656–1662.
Moody, M.E., Mack, R.N., 1988. Controlling the spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology 25, 1009–1021.
Morton, J.F., 1994. *Lantana*, or red sage (*Lantana camara* L. (Verbenaceae)), notorious weed and popular garden flower; some cases of poisoning in Florida. Economic Botany 48, 259–270.
Mucina, L., Rutherford, M.C. (Eds.), 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa (CD set).
Mune, T.L., Parham, J.W., 1967. The declared noxious weeds of Fiji and their control, 3rd ed. Fiji Department of Agriculture Bulletin, 48, pp. 1–87.
Nanjappa, H.V., Saravanane, P., Ramachandrappa, B.K., 2005. Biology and management of *Lantana camara* L.—a review. Agricultural Reviews 26, 272–280.
Neal, J., 1999. *Assessing the sterility of ornamental lantana varieties: are we exacerbating the weed problem?* Honors thesis, Department of Botany, University of Queensland, Brisbane.
Osunkoya, O.O., Perrett, C., 2011. *Lantana camara* L. (Verbenaceae) invasion effects on soil physicochemical properties. Biology and Fertility of Soils 47, 349–355.
Pandit, M.K., Pocock, M.J.O., Kunin, W.E., 2011. Ploidy influences rarity and invasiveness in plants. Journal of Ecology 99, 1108–1115.
Parisod, C., Holderegger, R., Brochmann, C., 2010. Evolutionary consequences of autopolyploidy. New Phytologist 186, 5–17.
Peng, M., Albrecht, J., Forer, P., 1999. Dynamic simulation of the spread of *Lantana camara* in a heterogeneous landscape. Proceedings of the International Symposium on Digital Earth. Science Press, pp. 1–8.
Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661.
Retief, E., 2010. Leaf-spot fungus fails to establish on *Lantana camara* in South Africa. Biocontrol News and Information 31, 21N–22N.
Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30, 409–431.
Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species—a global review. Diversity and Distributions 17, 788–809.
Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6, 93–107.
Richardson, D.M., Rouget, M., Henderson, L., Nel, J.L., 2004. Invasive alien plants in South Africa: macroecological patterns, with special emphasis on the Cape Floristic Region. Proceedings of the 10th MEDECOS Conference, April 25–May 1. Mill press, Rotterdam.
Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P., Hobbs, R.J., 2007. Riparian zones—degradation, alien plant invasions and restoration prospects. Diversity and Distributions 13, 126–139.
River Health Programme, 2003. State-of-rivers report: Hartenbos and Klein Brak Rivers. Department of Water Affairs and Forestry, Pretoria.
Sahid, I.B., Sugau, J.B., 1993. Allelopathic effect of Lantana (*Lantana camara*) and Siam Weed (*Chromolaena odorata*) on selected crops. Weed Science 41, 303–308.
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. Annual Review of Ecological Systematics 32, 305–332.
Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59, 19–32.
Sanders, R.W., 1987. Taxonomic significance of chromosome observations in Caribbean species of *Lantana* (Verbenaceae). American Journal of Botany 6, 914–920.
Sanders, R.W., 2006. Taxonomy of *Lantana* Sect. *Lantana* (Verbenaceae): I. Correct application of *Lantana camara* and associated names. SIDA 22, 381–421.
Sathish, R., Vyawahare, B., Natarajan, K., 2011. Antiulcerogenic activity of *Lantana camara* leaves on gastric and duodenal ulcers in experimental rats. Journal of Ethnopharmacology 134, 195–197.
Sharma, G.P., Raghubanshi, A.S., Singh, J.S., 2005. Lantana invasion: an overview. Weed Biology and Management 5, 157–165.
Singh, S.P., 1996. Biological control. In: Paroda, R.S., Chadha, K.L. (Eds.), 50 Years of Crop Science Research in India. Indian Council of Agricultural Research, New Delhi, pp. 88–116.
Spies, J.J., 1984. A cytotaxonomic study of *Lantana camara* (Verbenaceae) from South Africa. South African Journal of Botany 3, 231–250.
Spies, J.J., Stirton, C.H., 1982a. Chromosome numbers of the South African plants. South African Journal of Botany 48, 21–22.
Spies, J.J., Stirton, C.H., 1982b. Meiotic studies of some South African cultivars of *Lantana camara* (Verbenaceae). Bothalia 14, 101–111.
Stirton, C.H., 1977. Some thoughts on the polyploid *Lantana camara* L, (Verbenaccae). Proceedings of the Second National Weeds Conference. Balkema, Cape Town, pp. 321–340.
Swarbrick, J.T., Willson, B.W., Hannan-Jones, M.A., 1995. The biology of Australian weeds 25. *Lantana camara* L. Plant Protection Quarterly 10, 82–95.
te Beest, M., Stevens, N., Olff, H., Van der Putten, W.H., 2009. Plant-soil feedback induces shifts in biomass allocation in the invasive plant *Chromolaena odorata*. Journal of Ecology 97, 1281–1290.
te Beest, M., Le Roux, J.J., Richardson, D.M., Brysting, A.K., Suda, J., Kubešová, M., Pyšek, P., 2012. The more the better? The role of polyploidy in facilitating plant invasions. Annals of Botany 109, 19–45.
Thakur, M.L., Ahmad, M., Thakur, R.K., 1992. Lantana weed (*Lantana camara* var. *aculeata* Linn) and its possible management through natural insect pests in India. Indian Forester 118, 466–488.
Thaman, R.R., 1974. *Lantana camara*: its introduction, dispersal and impact on islands of the tropical Pacific Ocean. Micronesica 10, 17–39.
Urban, A.J., 2010. Lantana control recommendations. SAPIA News 16, 2.
Urban, A.J., Simelane, D.O., Retief, E., Heystek, F., Williams, H.E., Madire, L.G., 2011. The invasive "*Lantana camara* L". hybrid complex (Verbenaceae): a review of research into its identity and biological control in South Africa. African Entomology 19, 315–348.
Vahrmeijer, J., 1981. Poisonous plants of Southern Africa that cause stock losses. Tafelberg Publishers, Cape Town.
Van Oosterhout, E., Clark, A., Day, M.D., Menzies, E., 2004. Lantana control manual. Current management and control options for Lantana (*Lantana camara*) in the Australian state of Queensland. Department of Natural Resources, Mines and Energy, Brisbane, Qld, Australia. Available from URL: http://www.nrm.qld.gov.au/pests/wons/Lantana.
Van Wilgen, B.W., Richardson, D.M., Le Maitre, D.C., Marais, C., Magadlela, D., 2001. The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. Environment, Development and Sustainability 3, 145–168.
Van Wilgen, B.W., De Wit, M.P., Anderson, H.J., Le Maitre, D.C., Kotze, I.M., Ndala, S., Brown, B., Rapholo, M.B., 2004. Costs and benefits of biological

control of invasive alien plants: case studies from South Africa. South African Journal of Science 100, 113–122.

Van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M., Schonegevela, L., 2008. A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. Journal of Environmental Management 89, 336–349.

Van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotzé, J.D., Van den Berg, E., Henderson, L., 2012. An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. Biological Conservation 148, 28–38.

Van Wyk, B., Van Wyk, P., 1997. Field Guide to Trees of South Africa. Struik, Cape Town.

Walton, C., 2006. *Lantana camara* (shrub). Department of Natural Resources, Queensland, Australia & IUCN/SSC, Invasive Species Specialist Group (ISSG).

Wells, M.J., Stirton, C.H., 1988. *Lantana camara* a poisonous declared weed. Weeds A27, 1–7.

Wilson, B.W., 1995. Report on short term consultancy, Fiji 6–19 August 1995. SPC-German Biological Control Project, Brisbane.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J., Richardson, D.M., 2009. Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution 24, 136–144.

Zalucki, M.P., Day, M.D., Platford, J., 2007. Will biological control of *Lantana camara* ever succeed? Patterns, processes and prospects. Biological Control 42, 251–261.

Zoubiri, S., Baaliouamer, A., in press. *GC and GC/MS analyses of the Algerian* Lantana camara *leaf essential oil: effect against* Sitophilus granarius *adults*. Journal of Saudi Chemical Society. http://dx.doi.org/doi:10.1016/j.jscs.2011.01.013.

Edited by B-E Van Wyk